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Mice pollinate the Pagoda Lily, *Whiteheadia bifolia* (Hyacinthaceae) — First field observations with photographic documentation of rodent pollination in South Africa

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Abstract

For the first time in South Africa nocturnal rodent pollination was observed and photographed under natural conditions. In the Northern Cederberg area of the Western Cape field studies and experiments showed that flowers of *Whiteheadia bifolia* (Hyacinthaceae) are visited at night by rodents, mainly the Namaqua Rock Mouse *Aethomys namaquensis*. The mice were observed licking nectar while being dusted with pollen and touching the stigmas. No other visitors were observed during the day or night. *W. bifolia* pollen was found around the snouts and in the faeces of live-trapped mice, the latter likely as a result of grooming their fur, since they visited the flowers without eating or destroying them. *W. bifolia* has characters of the rodent pollination floral syndrome such as visually inconspicuous, bowl-shaped flowers close to the ground, with stiff stamens as well as easily accessible, very viscous nectar and a weak, slightly sourish-nutty scent. Furthermore, these findings support the hypothesis that pollination syndromes can be used to make testable predictions about floral trait evolution due to pollinator selection.

Keywords: Floral syndrome; Hyacinthaceae; Rodent pollination; Therophily; Western Cape of South Africa; *Whiteheadia bifolia*

1. Introduction

Using South Africa as an example, Stefan Vogel (1954) introduced his concept of 'pollination syndromes', a specific combination of floral traits having evolved in adaptation to special pollinator guilds. Vogel distinguished guilds of flies, long-tongued flies and butterflies, moths, bees as well as birds. Later, special forms were added such as the spectacular oil-collecting bees (Vogel, 1974) or even an absolutely unexpected group of pollinators, namely rodents (Wiens and Rourke, 1978). In South Africa the phenomenon of rodent pollination was first discovered in the genus *Protea* (Proteaceae) (Rourke and Wiens, 1977; Wiens and Rourke, 1978) and has subsequently been documented only in *Massonia depressa* (Hyacinthaceae), two *Androcymbium* species (Colchicaceae), *Cytinus visseri* (Cytinaceae) and *Liparia parva* (Fabaceae) (Johnson et al., 2001, 2008; Kleizen et al., 2008, 2009-this issue; Letten and Midgley, 2009).

Rodents are part of a group of pollinating animals that are known as 'non-flying mammals' to differentiate them from bats. This group includes mainly marsupials (Australia, New Guinea, Neotropics), primates (mainly monkeys in tropical Africa and the Neotropics and lemurs in Madagascar) as well as rodents (beside South Africa also tropical Africa, China, India, Malaysia, Australia and the Neotropics) (Vieira et al., 1991; Hopkins, 1992; Carthew and Goldingay, 1997; Yumoto et al., 1999; Tandon et al., 2003; Wang et al., 2008).

Non-flying mammal pollination was first suggested by Kerner von Marilaun (1891), and later demonstrated in various studies (Porsch, 1934, 1935, 1936a,b, and citations therein; Coe and Isaac, 1965). Porsch (1935) and several authors later defined a 'syndrome' of floral characters that indicate adaptation to non-flying mammals (therophily) (Carthew and

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Goldingay, 1997). However, mammal morphology and behaviour varies greatly, resulting in a wide range of floral adaptations. Thus, rodent pollination can be distinguished from pollination by non-flying mammals. The most common characters of rodent-pollinated flowers are inconspicuous dull colouration, often geoflory, robustness, exserted reproductive organs, easily accessible ample amounts of sometimes viscous nectar, yeasty or musty scent and nocturnal anthesis, nectar and scent emission (Rebelo and Breytenbach, 1987; Johnson et al., 2001).

In the present study the 'Pagoda Lily' *Whiteheadia bifolia* (Jacq.) Baker (Hyacinthaceae) is hypothesised to be pollinated by rodents on the basis of sharing most of the abovementioned characters (see also Manning et al., 2002). Thus, the aims of this paper were to study the pollination biology of this species in order to test this hypothesis. Since all previous studies of rodent pollination in South Africa relied mainly on indirect evidence, the main focus was on direct observations under natural conditions (see also Wester, 2009). The findings are discussed in the context of the debate concerning the utility of pollination syndromes.

2. Materials and methods

2.1. Plants and study site

W. bifolia is restricted to the arid winter-rainfall region of South Africa and Southern Namibia. Observations and live trapping of mice took place from 17 July to 7 August 2008 at a ~0.25 ha plot along the Sevilla rock art trail on Travellers Rest Farm, Agter-Pakhuis in the northern Cederberg area of South Africa (S 32° 04' 31.52″, E 19° 04' 48.42″; elevation 320 m). Here, several (~100) individual plants occurred in shady rock crevices and cavities (Fig. 1A, B).

2.2. Observations

Several *W. bifolia* plants were observed for potential visitors in the field, 13.5 h in total over 5 nights between 6:30 p.m. and 2 a.m., and 5 h in total during the day (over 2 days) between 10 a.m. and 6 p.m. Torch lights were covered with red plastic film. Additionally, a video camera, 1 m away from *W. bifolia* plants, recorded non-stop for 4.5 h in total on two nights between 7 p.m. and 2 a.m. The inflorescences were illuminated by the camera display light, also covered with red plastic film. In addition, foraging behaviour of captured mice that were released in two glass terraria, was observed for ~10 h over 3 nights between 8 p.m. and 2 a.m. Each terrarium was equipped with a 5 cm deep layer of sand, several stones providing hiding places and two flowering *W. bifolia* plants. Only one mouse was released per terrarium.

2.3. Trapping of rodents and pollen loads

Rodent traps, baited with a mixture of peanut butter and rolled oats, were laid out near *W. bifolia* plants. In the late afternoon 30 traps were set up over 7 nights. Traps were checked at night, and in the early morning. Captured rodents were removed, identified and marked with a felt pen on the tail.

On two nights captured rodents were removed just after trapping and were temporarily put in plastic bags with a small hole in one corner. The snouts protruded through the holes, allowing the fur to be swabbed with a small block of fuchsin glycerine gelatine (Beattie, 1971). Each of the samples was then melted onto a microscope slide and examined microscopically for the presence of pollen.

Rodent faeces were collected from 30 traps and stored in a fridge. Each sample was mixed with water and vortexed for 10 min. Then fuchsin gelatine was added and the samples were centrifuged for 5 min at 2000 rpm in order to compact the pollen into a solid layer. A part of the compacted layer was mounted on a slide and examined microscopically for the presence of pollen.

In order to test for pollinator movement between plants, *W. bifolia* inflorescences were dusted by means of a brush with one of four colours of fluorescent dye over a period of two days at sunset. Thereby it was made certain that the plants were only touched with the brush. Traps were laid out near the study plants. Later in the night the treated and also untreated surrounding inflorescences as well as the captured mice were checked for dye under ultraviolet lamps.

2.4. Floral characters

Floral measurements (to the nearest 0.5 mm) were taken from 6 adult flowers, each of them sampled from a different plant. Height of the curved stamens was measured as chord (straight-line distance) from the bottom of the 'filament-bowl' to the distal end of the anthers.

Volume and sugar concentration of floral nectar was measured as standing crop on 3 days (12 a.m., 5–11 p.m.). The volume of nectar was measured with microcapillary tubes (Brand, Wertheim, Germany). Sugar concentration was measured using a hand held refractometer (Eclipse 45-81: 0–50% and Eclipse 45-82: 45–80% sucrose w/w, Bellingham and Stanley, Kent, UK). Two samples of nectar were spotted onto filter paper, air dried and then stored in a fridge for later determination of free sugars. The nectar sugars were eluted (2 samples combined) from the filter paper by adding two times 300 µl ddH_2O. The sample was vortexed and incubated for 10 min at room temperature, centrifuged, the supernatants combined and freeze dried, dissolved in pyridine and derivatised with methoxyamine and MSTFA. The sample was analysed by a GC-MS system (gas chromatograph Agilent 6890N interfaced to a mass spectrometer Agilent 5975), equipped with a DB-5 column (30 m long, 0.25 mm inner diameter, 0.25 µm film thickness). The operational conditions were as follows: injection volume 1 µl, injector temperature 280 °C, split ratio 1:5, constant flow 1 ml/min, carrier gas helium; temperature programme: 70 °C to 76 °C at a rate of 1 °C/min, then at a rate of 5 °C/min to 310 °C, hold for 8 min; MS transfer 280 °C, EI mode (electron energy 70 eV), scanning mass range 40 to 550 *m/z*. Component identification was carried out by comparison of GC retention times with those of reference standards and was confirmed by mass spectra. The GC-MS data were processed using the MSD ChemStation

Fig. 1. *Whiteheadia bifolia*: (A) Rocky habitat in the northern Cederberg near the Brandewyn river with plants in the rock crevices; (B) Plant growing in rock crevice with broad axis and inflorescence near the ground, large green bracts and inconspicuous flowers; (C) *Aethomys namaquensis* (Namaqua Rock Mouse) visits *W. bifolia* flowers in the field; (D) *A. namaquensis* laps nectar with its pink tongue and gets dusted with pollen around its nose; (E) An unidentified mouse laps nectar out of a flower; (F) Flowers in the axis of large green bracts with whitish-green tepals, style and thick curved stamens, their filaments broadened at their base and forming a 'stamen bowl'. Bars = 3 cm in B, 0.5 cm in F. D and E taken in a terrarium. (photographs: P. Wester)

D.02.00.237 software (Agilent), component identification was carried out using the NIST 2005 mass spectral data base (NIST/EPA/NIH mass spectral library 2.0., Gaithersburg, USA). Viscosity of the nectar was checked qualitatively during the day and night. Floral scent was qualitatively checked at 8–11 p.m. on 4 days.

3. Results

3.1. Floral visitors and their foraging behaviour

Aethomys namaquensis A. Smith (Namaqua Rock Mouse, family Muridae) was observed regularly visiting *W. bifolia* flowers in the field at night. More than 25 flower visits were observed at three nights between 7 p.m. and 1 a.m. (Fig. 1C). As far as could be identified in the field at least 2 different individuals of the Namaqua Rock Mouse were observed. In the terrarium experiment Namaqua Rock Mice (Fig. 1D; Appendix: Slides 1–3) and one unidentified mouse (family Muridae; Fig. 1E; Appendix: Slides 4–8) were observed. The mice hid themselves between rocks after release, but emerged at night (11 p.m.–2 a.m.) and without hesitation they went to the flowers of several different inflorescences (more than 50 times in total). In the field and in the terrarium the mice visited flowers and inflorescences one after another, returning to the same inflorescence after a few minutes. The mice spent several seconds at each flower. They pushed their nose and snout on or between the curved stamens and licked the nectar between the ovary and the stamens with their tongue (Fig. 1D, E; Appendix: Slides 3, 5–8) and were dusted with pollen on the snout (Fig. 1D; Appendix: Slides 1–3, 5). The pollen-coated area around the snout made contact with the stigmas of the flowers. The mice only lapped the nectar and did not feed on pollen directly or eat, damage or destroy the flowers. When visiting the flowers, the mice mostly held on to the large bracts (Fig. 1D; Appendix: Slides 1, 3, 7–8). No other flower visitors were observed in the dark or at daytime during numerous hours spent near the plants. No visitors were recorded with the video camera at night.

There was no clear evidence of movement of the fluorescent dye powder between inflorescences or dye on caught mice. A few times it was observed that mice went towards the dyed *W. bifolia* inflorescences, but just before reaching them, turned round.

3.2. Trapping of rodents and pollen loads

A total of 55 mice were caught in the study area. Initially, 54 were identified as *A. namaquensis* and one as *Graphiurus ocularis* A. Smith (Spectacled Dormouse, family Gliridae). Closer investigation of photographic material resulted in identification of an individual that appeared uncharacteristic of an *A. namaquensis* (Fig. 1E). Consistent identification from the photographs was not possible; the species is possibly *Myomyscus verreauxi* A. Smith (Verreaux's Mouse), but *Aethomys granti* Wroughton (Grant's Rock Mouse) and *A. namaquensis* cannot be ruled out (M. Avery, G. Bronner, C. Chimimba, D. Hamerton, K. Medger, J. Nel, G. Palmer, T. Robertson, P. Taylor, pers. comm.). Ten of the mice were recatches. Out of the seven snout samples, six contained *W. bifolia* pollen (4, 4, 7, 26, ~500, >1000 pollen grains). In three of the samples less than 10 pollen grains of another plant species was found (unidentified Asteraceae), in one sample only one pollen grain of a further unidentified species. Out of 29 faecal samples, 28 contained *W. bifolia* pollen (mean: 23 pollen grains per dropping, range: 0–131, SD: 30). Only few pollen grains of other plant species were found (unidentified Asteraceae: less than 6 pollen grains in 5 out of 13 samples, further unidentified species: less than 16 pollen grains in 5 out of 13 samples). There were no pollen grains in the faeces of the Spectacled Dormouse.

3.3. Floral characters

W. bifolia in the study site was observed to be flowering between mid July till mid August. Several flowers with large green, relatively sturdy bracts are arranged along the very broad and stable axis (Fig. 1B). The cup-shaped flowers are held near the ground, and have inconspicuous whitish-green colouration (Fig. 1B, F). The 6 stamens are thick, stiff and robust. The connection between the filament and the anthers is solid and the anthers are not versatile (Fig. 1F). The stamens are 8.6 mm (7–9.5 mm, SD: 0.9) in height and 5 mm (4–6 mm, SD: 0.7) apart. The filaments are broadened and fused at their base to form a kind of bowl, which contains the nectar (Fig. 1F). This 'stamen bowl' has an inner diameter of 7.6 mm (6.5–9 mm, SD: 0.9) and a height of 2.3 mm (2–2.5 mm, SD: 0.3). The style is 8.6 mm in height (7–9.5 mm, SD: 1). The distance between pollen-sac and stigma is 1.7 mm (0.5–3 mm, SD: 0.9).

Nectar volume and concentration were very variable (volume: 7.9 µl ± 5.9 SD, range: 1.6–22 µl; sugar concentration: 27% ± 13.9 SD, range: 10–64%; $n = 23$ flowers and 16 plants). The nectar was extremely viscous. The sugars consisted of 7% sucrose, 27% glucose, 66% fructose, and 0% xylose.

Sometimes floral scent was detected as a weak, somewhat sourish-nutty smell, similar to slightly rancid butter, but often also no scent was detectable.

4. Discussion

4.1. Proof for rodent pollination

The present study confirms the original hypothesis that *W. bifolia* is rodent-pollinated. Direct field observations, supported by detailed observations of captured mice in terraria, showed that mice purposefully targeted inflorescences of different *W. bifolia* plants one after another. They visited the flowers eagerly, licked up the nectar and transferred pollen between plants on their snouts. Foraging behaviour at the flowers was non-destructive. No other visitors were observed.

The present study is the first known observation and direct photographic record of nocturnal rodent pollination under natural conditions in South Africa (see also Wester, 2009), although stated that this is virtually impossible (Wiens et al., 1983). In daylight Paterson-Jones (2007) incidentally noted a single *Rhabdomys pumilio* (Four-striped Grass Mouse) visiting

Protea species and Johnson et al. (2001) observed an individual Namaqua Rock Mouse feeding on *Massonia* flowers after being released into the field after a terrarium experiment. Letten and Midgley (2009) recorded a flower visit by an unidentified rodent using a short video sequence of an automatic surveillance system. Also outside South Africa, pollinating nocturnal rodents were observed and photographed in the field in Central America (Costa Rica; Lumer, 1980), West Africa (Cameroon; Grünmeier, 1990) and recently in China (Wang et al., 2008).

Field observation was supplemented with indirect evidence. Copious amounts of *W. bifolia* pollen were found around the snouts and in the faeces of almost all captured mice. This pollen in the faeces was likely ingested after grooming, since it was observed in the field and in captivity that the mice did not feed directly on pollen (see also Fleming and Nicolson, 2002).

In contrast to other studies (e.g. Wiens et al., 1983; unpubl. data, AP), fluorescent dye was actively avoided by the mice in the present study. One can speculate that reflectance, composition or odour of dye could have been a deterrent.

4.2. The rodent perspective

The observed Namaqua Rock Mouse and the Verreaux's Mouse are known as visitors of several species of *Protea* (Wiens and Rourke, 1978; Biccard and Midgley, 2009-this issue). The Namaqua Rock Mouse is also known to visit *Androcymbium* species (Kleizen et al., 2008) and *M. depressa* (Johnson et al., 2001). In the present study a further rodent, the Spectacled Dormouse (*G. ocularis*), was caught once, but no pollen was found in the faeces. The species has been caught near *Protea amplexicaulis* and carried pollen around the snout (Wiens and Rourke, 1978). Future studies might prove that it also pollinates *W. bifolia*.

Nectar (and maybe pollen) of *W. bifolia* and other rodent-pollinated Cape plants might be an important energy source for Namaqua Rock Mice in the late winter breeding season when other resources are scarce (Wiens et al., 1983; Fleming and Nicolson, 2002). However, it is important to note that the Namaqua Rock Mouse and Verreaux's Mouse are omnivorous (Skinner and Chimimba, 2005), and thus have access to a wider range of other resources. Furthermore, floral resources are spatially and temporally restricted (Wiens et al., 1983). Thus morphological and behavioural adaptations for flower feeding on the rodent's side are unlikely (Wiens et al., 1983). This is in contrast to the marsupial Honey Possum *Tarsipes rostratus* (Tarsipedidae) in Australia, which exhibits morphological, physiological and behavioural adaptations for flower feeding (Wiens et al., 1979).

4.3. The plant perspective

The habitat of *W. bifolia* overlaps with that of the Namaqua Rock Mouse (and the Spectacled Dormouse) (Skinner and Chimimba, 2005; Channing, 1984), and the species shows characters that are likely adaptations to rodent pollination. These include winter flowering, which corresponds with the time of food shortage and the breeding season of Namaqua Rock Mice and several floral characters that fit the mice's behaviour and morphology: The flowers are arranged in an inflorescence close to the ground, reachable by mice. Such geoflory is also found in certain *Protea* and *Androcymbium* species, *M. depressa*, *C. visseri*, *L. parva* and *Cajophora coronata* (Loasaceae in Argentina) (Wiens and Rourke, 1978; Cocucci and Sérsic, 1998; Johnson et al., 2001, 2008; Kleizen et al., 2008; Letten and Midgley, 2009). The flowers of *W. bifolia* are not conspicuously coloured and thus in this regard unattractive to insects and birds. Visual conspicuousness is not necessary in the dark when rodents are normally active. Visually inconspicuous flowers are also found in certain *Blakea* (Melastomataceae in Costa Rica) and *Protea* species, *M. depressa* and *Androcymbium scabromarginatum* (Wiens and Rourke, 1978; Lumer and Schoer, 1986; Johnson et al., 2001; Kleizen et al., 2008). Contrasting to *W. bifolia*, some other rodent-pollinated species (*Blakea* and *Protea* spp., *A. scabromarginatum*) are cryptic in terms of being covered by stems, leaves or bracts (Wiens and Rourke, 1978; Lumer, 1980; Kleizen, 2008), interpreted also as a possibility not to attract unwanted visitors (Rebelo and Breytenbach, 1987). The whole plant of *W. bifolia* is very robust, especially the stamens. Thus, the flowers are not damaged by flower-visiting mice. Stiff flower parts such as stamens and styles are also reported for some *Protea* species and *M. depressa* (Rourke and Wiens, 1977; Johnson et al., 2001). In the cup-shaped flowers of *W. bifolia* nectar is easily accessible. The height of stamens and style, which corresponds more or less to the distance between the nectar and the distal end of the reproductive organs, is approximately 9 mm. This distance fits to the so-called '10 mm rule' of rodent-pollinated species that is said to correspond to the rostrum length of the pollinator (Wiens et al., 1983). However, at least in *W. bifolia* it seems to be more or less the critical distance/position enabling the mice to reach the nectar with their tongue in combination with touching the reproductive organs around their snout or nose.

Nectar volume in *W. bifolia* was lower than volumes often reported for other rodent-pollinated species (Lumer, 1980; Cocucci and Sérsic, 1998; Johnson et al., 2001; Kleizen et al., 2008), but was similar to *L. parva* (Letten and Midgley, 2009) and some *Protea* species (similar per flower, but more in *Protea* spp. per inflorescence, Wiens and Rourke, 1978). Similar to findings in other rodent-pollinated plants (e.g. Letten and Midgley, 2009) nectar volume in *W. bifolia* was very variable. Although the volume in *W. bifolia* was sometimes low, the mice visited the flowers heavily. Only at the end of the flowering time when little (or no) nectar remained, did visits decline.

Nectar concentration in rodent-pollinated flowers is described to be low (Cocucci and Sérsic, 1998; Johnson et al., 2001; Letten and Midgley, 2009), but also sometimes higher (Wiens et al., 1983; Fleming and Nicolson, 2003; Kleizen et al., 2008; Biccard and Midgley, 2009-this issue; this study). Nectar sugars of *W. bifolia* are hexose-dominant and had no xylose. The nectar composition differs from that of other rodent-pollinated species that typically have sucrose-rich nectar (*Blakea*, *Protea* spp., *M. depressa*) and xylose (*Protea* spp. and *M. depressa*) (Lumer, 1980; Wiens et al., 1983; Nicolson and Van Wyk, 1998; Johnson et al., 2001).

The nectar in *W. bifolia* was extremely viscous and sticky. Preliminary data show a viscosity, calculated from capillary descent times (after Heyneman, 1983) that was at least 50 to >100 times that of a solution of an equivalent sugar concentration given in Fasman (1976) (unpubl. data, PW). As the quantity of the nectar was often low but the flowers were visited regularly, uptake of the viscous nectar might function in low amounts like a lollipop. Viscous nectar in rodent-pollinated plants was also found in *Androcymbium* (Midgley, pers. comm.; Kleizen et al., 2008), *M. depressa* (described as jelly-like, Johnson et al., 2001) and *Blakea chlorantha* (described as mucilaginous, Almeda, 1980). In other rodent-pollinated species there seems to be no evidence that the nectar is highly viscous (e.g. *L. parva*: Midgley, pers. comm.; *Protea* spp.: Wiens et al., 1983; but see Fleming and Nicolson, 2003). Viscosity in nectar might prevent flower visits of nectar stealing insects. Although nectar in *W. bifolia* was exposed, insects were never observed visiting the flowers. Uptake of such thick sticky nectar could be difficult for the insect's narrow mouthparts (see Betts, 1930; Waller, 1972; Heinrich, 1975; Harder, 1986). Birds in general prefer more diluted nectar (see Wiens et al., 1983; Johnson and Nicolson, 2008), but are able to handle viscous nectar (Evans, 1996). In this study birds were never observed visiting the flowers, possibly because of the lack of attractiveness (e.g. colouration). Slimy nectar is often found in bat-pollinated flowers (Van der Pijl, 1936; Vogel, 1958). Frugivorous bats might occur (or migrate) in the area, such as the Straw-coloured Fruit Bat *Eidolon helvum* (DeFrees and Wilson, 1988) or the Egyptian Rousette *Rousettus aegyptiacus* (family Pteropodidae, Megachiroptera), both species also known for drinking nectar and pollinating flowers at least in West Africa (Baker and Harris, 1959; Grünmeier, 1990). However, other floral characters of *W. bifolia*, such as geoflory, relatively small flowers, weakness of scent and relatively low amount of nectar are not attractive to bats (Van der Pijl, 1936; Vogel, 1958).

Floral smell seems to play a major role as attracting mechanism in rodent-pollinated plants as the flowers are visually inconspicuous (see also Porsch, 1935; Rourke and Wiens, 1977; Johnson et al., 2008). Rodent-pollinated species mostly have a distinctive yeasty, musty, nutty or sourish odour (Porsch, 1935; Rourke and Wiens, 1977; Rebelo and Breytenbach, 1987; Biccard and Midgley, 2009-this issue), but odour can be absent or not noticeable (Lumer, 1980). In *W. bifolia* the smell of the flowers was weak, slightly sourish-nutty and also often not detectable (see also Manning et al., 2002). However, this does not exclude the existence of an odour attractive to rodents due to their well developed sense of smell (Lumer, 1980; Stoddart, 1980).

4.4. Floral syndrome of rodent pollination

The rodents show no clear adaptation to *W. bifolia*. However, *W. bifolia* has a specific combination of floral characters consistent with the rodent pollination syndrome (geoflory, visual inconspicuousness, bowl-shaped, robust flowers, easy accessible, very viscous nectar and a slightly sourish-nutty smell). This shows convergence with other rodent-pollinated species mentioned above that have likely evolved as adaptations to rodent pollinators (see also Wiens et al., 1983). Similar, convergent character combinations indicate that there are further candidates being rodent-pollinated. One example of the same family Hyacinthaceae (beside *W. bifolia* and *M. depressa*) is the Pineapple Lily *Eucomis regia* (unpubl. data; Shuttleworth and Johnson, 2009). In contrast, the second species of the genus *Whiteheadia*, the Namibian *W. etesionamibensis* U. Müll.-Doblies & D. Müll.-Doblies, has honey-scented, white flowers that suggest insect pollination (see Müller-Doblies and Müller-Doblies, 1997).

Recently the applicability and consistency of the pollination syndrome concept (Vogel, 1954; Faegri and Van der Pijl, 1979) was criticised (Waser et al., 1996; Ollerton et al., 2009). However, as demonstrated in other studies, the present study has shown that floral syndromes are a useful guide in the formulation of testable hypotheses about the identity of unknown pollinators (e.g. Consiglio and Bourne, 2001; Hargreaves et al., 2004; Martén-Rodríguez et al., 2009).

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Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.sajb.2009.07.005.

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